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LIFE HISTORY AND DEMOGRAPHY OF A TWIG EPIPHYTE: A CASE STUDY OF *ERYCINA CRISTA-GALLI* (ORCHIDACEAE)

DEMETRIA MONDRAGÓN,* CITLALLI MALDONADO, AND REMEDIOS AGUILAR-SANTELISES

Centro Interdisciplinario de Investigación para el Desarrollo Integral Regional (CIIDIR) unidad Oaxaca. Calle Hornos No. 1003, Santa Cruz Xoxocotlán, Oaxaca. México. C.P. 71230.
Email: dmondragon@ipn.mx

ABSTRACT. Little is known about the life history of twig epiphytes or about the demographical responses they have developed in order to survive in such an oligotrophic and often disturbed environment. In order to develop a model to further the understanding of the demographical adaptations of this type of plant, we present demographic data of *Erycina crista-galli,* and compare it with other epiphytes. In July 2004 two populations were selected: Unión Roja (UR) and Santo Domingo (SD). 563 individuals were marked in SD and 592 in UR. The survival rates were: 0.439 seedlings, 0.22 juvenile, 0.49 reproductive$_1$, and 0.49 reproductive$_2$ for SD and 0.25 seedling, 0.41 juvenile, 0.32 reproductive$_1$, and 0.45 reproductive$_2$ for UR. The highest pseudobulb production rates were presented by reproductive$_1$ in SD (1.47 ± 1.04), and by reproductive$_2$ in UR (0.94 ± 1.10), while the seedling (0.37 ± 0.26 cm/year SD) was the life stage that showed the highest increase. The fecundities were of 1.00 ± 0.00, and 2.00 ± 0.00 capsules/individual in reproductive$_1$ and of 2.00 ± 1.73, and 2.00 ± 2.00 capsules/individual in reproductive$_2$. Both populations were decreasing (λ = 0.5 SD and λ = 0.398 UR). The highest elasticity values were for r_2 (0.702 SD and 0.324 UR). There was no consistent difference in the elasticity values of fecundity, growth and stasis between *E. crista-galli* and the other species. The only demographic feature that appears to distinguish twig epiphytic orchids from other epiphytic orchids is the age of sexual maturity.

Key words: Coffee plantation, matrix analysis, Mexico, population dynamics, epiphyte ecology, Soconusco

INTRODUCTION

The influential aspects of the hosts where epiphytes thrive, include a) the branching system of the host, b) the diameter and inclination of the branches, c) the texture and pH of the bark, d) the quantity of light that reaches the internal part of the treetop in function of the quality and quantity of foliage, and e) the size and age of the branches, etc. (ter Steege & Cornelissen 1989, Rudolph et al. 1998, Zotz et al. 1999, Isaza et al. 2004). These host characteristics, together with the micro-environmental conditions of light, humidity, and temperature of the different parts of the host and the ecophysiological requirements of the epiphytes (Bennett 1988, Zotz 1997, Zotz et al. 1999, Graham & Andrade 2004, Jácome et al. 2004), determine the distribution pattern of the epiphytes upon the host.

Among epiphytes, there is a small group which is restricted to the smallest and thinnest branches of their hosts (zone V, according to the Johansson's classification, 1974). These branches receive high doses of sunlight radiation, the atmospheric humidity surrounding them is low, and there is a low accumulation of minerals (Johansson 1974, Chase 1987, Benzing 1995). These plants are known as "twig epiphytes" and present anatomical and physiological adaptations (deciduous leaves, seeds with protuberances of the testa, modified cells in the velamen of the root, among others) that allow them to survive in this stressful environment but that, at the same time, could be restricting their distribution to other parts of the tree (Chase 1987, Benzing 1995).

Very little is known about the demographical responses that twig epiphytes have developed to be able to survive in this environment (Calvo 1993) that, as its name indicates, is limited to the thinnest branches of the hosts, which are more susceptible to breakage. This habitat fragility demands that its inhabitants rapidly reach reproductive age, in order to produce seedlings that colonize new branches and to persist in such a dynamic environment. This selection pressure has caused twig epiphytes to develop demographical responses different from other epiphytes, which are characterized by low growth rates and a high survival of adult individuals (Zozt 1995, Hietz 1997, Tremblay 2001, Mondragón et al. 2004). Chase (1987), in his studies on twig epiphytism in the genus *Oncidium* and other neotropical orchids, mentioned that these plants have short life cycles and may reach maturity in less than a year; however, this author

* Corresponding author.

does not analyze their demographical rates. Calvo (1993), in his study about the evolutionary demography of *Tolumnia variegata,* in which he analyzed the population dynamic of that species by tree years using matrix analysis, found that an increase in seedling production could increase the fitness of the population, and that only very high increases of fruit production cause a reduction in the future growth and flower production of the individuals.

The objective of the present work is to present the general characteristics of the life history and demography of a twig epiphyte, to help us to understand the responses of this type of epiphyte to its environment, as compared to other kinds of plants that grow in more stable environments that are richer in nutrients and water (Rudolph et al. 1998, Hietz et al. 2002). We attempt to answer questions such as: Do twig epiphytes reach sexual maturity earlier than epiphytes of larger branches? Is the survival of adult individuals as important as it is for other epiphytes? Do twig epiphytes have higher rates of recruitment?

Methods

The sites of study were the following:

Santo Domingo (SD) located in the municipality of Unión Juárez, Chiapas, México (92°06′21″W; 15°01′48″N), with an altitude of 850 m.a.s.l. The weather is semitropical-humid AC (m), with a 27.8°C average annual temperature, seasonal rains from May to October, and a total annual precipitation of 2478 mm. Santo Domingo has fragments of tropical rain forest and extensive plantations of shade coffee (INEGI 2000), which can be classified as "modern" monoculture, production systems with *Inga* sp. (Fabaceae) as shade, according to the classification proposed by Moguel and Toledo (1999) for the coffee production systems in Mexico. However, some plots could be classified as commercial polycultures, as they also have banana and mamey trees (*Manilkara zapota* (L.) P. Royen, Sapotaceae) and other fruit trees.

Unión Roja (UR) is located in the municipality of Cacahoatán at 480 m.a.s.l. (14°59′N; 92°10′W). The weather is warm-humid AC (m) with a 25.4°C mean temperature and a 4720 mm mean total annual precipitation. Vegetation is a mixture of fragments of tropical rain forest combined with coffee plantations, of the same kind as in Santo Domingo.

Management coffee regimens at both localities consist in annual pruning, where old branches are cut, and the mosses and epiphytes growing at the trunk and lowest branch of the coffee shrub are removed. Coffee shrubs are replaced every four or five years by new one-year shrubs.

Erycina crista-galli ((Rchb. f.) N.H.Williams and M.W.Chase) is classified, just as every other species of *Erycina,* as a twig epiphyte (Chase et al. 2005). It is a small deciduous species, 5–8 cm tall with thin, soft leaves arranged in a fan and filiform roots 0.5–0.7 mm in diameter. Pseudobulbs are compressed with one apical, abortive leaf and several leafy, distichous, imbricate sheaths at the base; the blades of the leaves are narrowly elliptical and acute. Inflorescences are basal, appearing from the axils of the upper sheaths, 3–4 per pseudobulb, racemose, with 1–3 flowers which open sequentially and have amplexicaul floral bracts. The flowers are showy and very large in proportion to the size of the plant; the sepals are greenish-yellow, and the petals are yellow with a few orange-yellow spots near the base. The capsules are obovoid to ellipsoid. *Erycina crista-galli* is distributed from México, through Central America to Peru and Colombia, and found growing in montane rain forests and coffee plantations, from 650–1850 m (Hágsater & Salazar 1990).

In July 2004 in each of the two sites, one population was selected (defined as a set of coffee shrubs where the density of *E. crista-galli* was > ten individuals/shrub). Within each of the populations, all the coffee plants were marked (29 in SD and 35 in UR) to facilitate continued recognition during the experimental period. Individuals of *E. crista-galli* were also marked with a numbered label. For each individual of *Erycina,* the number of pseudobulbs was counted, the height of the largest pseudobulb was measured, and the number of inflorescences, flowers and capsules was registered. In June 2005, all the same variables were taken from the marked individuals, taking note also of mortalities and recording the cause according two categories: dried or disappeared (due to the breaking of the twig where they grew, or that they fell or were removed), as well as the number of new seedlings that had been recruited.

The individuals of *E. crista-galli* were classified in four stages (Table 1), and annual demographic parameters were calculated using the data taken in the 2004 and 2005 census. The survival rates per stage were calculated by dividing the number of individuals cataloged in the *n* stage during 2004 by the number that survived until 2005. The individual growth rate was calculated in two ways: by the production of pseudobulbs and by the increase in height of the largest pseudobulb. These rates were calculated for each of the individuals subtracting the 2005 value from the 2004 value to obtain the mean and the standard deviation for each stage.

Different fecundity components of these plants were evaluated: the proportion of individ-

TABLE 1. Description of the stages of the life cycle of *Erycina crista-galli* according to characteristics of pseudobulb size and reproductive structures.

Stage	Morphological and reproductive characteristics
Seedlings (s)	One pseudobulb ≥0.01–0.19 cm in height; intense green color; leafless.
Juvenile (j)	One pseudobulb of 0.2–0.39 cm in height; no reproductive structures.
Reproductive$_1$ (r_1)	One pseudobulb ≥0.4 cm in height; with or without reproductive structures; with 2 to 6 fully developed linear leaves of an intense green color during raining season; or leafless or with evidence of the latter during dry season.
Reproductive$_2$ (r_2)	Individuals with 2 or more pseudobulbs; with or without reproductive structures; with 2 to 6 very developed linear leaves per bulb, of intense green color during raining season; or leafless or with evidence of the latter during dry season.

uals that reproduced within each category, the average production of inflorescences per individual, and the average production of capsules per reproductive individual. The fecundities included in the cycle were calculated based upon the proportion of seedlings found on the sampled coffee bushes in June 2005, which would correspond to each one of the individuals cataloged as reproductive$_1$ and reproductive$_2$ respectively.

The intrinsic rates of growth of the populations (λ) were calculated by the construction of Lefkovitch type matrices (Caswell 1989). We also calculated the stable structures and the reproductive values of each population. The respective elasticity matrices were constructed.

To determine the importance of the different demographical processes over λ for these orchids, the elasticity values found in this study were compared with those reported for epiphytic orchids on thick branches: *Artorima erubescens, Lepanthes caritensis, Lepanthes eltoroensis, Laelia speciosa* (Hernández-Apolinar 1992, Tremblay 1997, García-Soriano 2003, and Tremblay & Hutchings 2003). Features of the places of study of those plants can be seen in TABLE 2. To that end, the elasticity values per process (stasis, growth, fecundity) were summed up, according to the methodology proposed by Silvertown et al. (1993). Likewise, to compare the importance of the different stages over λ, we grouped the values for the four life stages in three sections: seedlings, non-reproductive stages, and reproductive stages. These were summed, obtaining a value for each of the sections.

RESULTS

In the Santo Domingo site 563 individuals were marked: 41 seedlings, 50 juveniles, 246 reproductive$_1$, and 226 reproductive$_2$; and 592 were marked in UR: 4 seedlings, 32 juveniles, 25 reproductive$_1$, and 531 reproductive$_2$. Both sites are dominated by reproductive individuals.

In SD, the reproductive individuals presented the greatest increase in the number of pseudobulbs, especially the reproductive$_1$ individuals, which almost duplicated the number of pseudobulbs (TABLE 3). However, although in UR the reproductive$_1$ also produced the most pseudobulbs, the reproductive$_2$ had a decreased growth rate. The greatest growth rates, as measured by height increase of the pseudobulbs, occurred in the non-reproductive stages: the seedlings in SD and the juveniles in UR.

Of the 246 individuals cataloged as reproductive$_1$, in SD, only 27 presented some kind of reproductive structure (inflorescence or vestiges of inflorescences). This proportion was larger in the reproductive$_2$ where 115 of the 226 showed reproductive structures, while in UR only one of the 17 reproductive$_1$ and 271 of the 531 reproductive$_2$ presented reproductive structures. In both populations we observed that the reproductive$_2$ were those which produced the most inflorescences and capsules.

Of the 563 marked individuals in SD in 2004,

TABLE 2. Features of the places of study of the orchid species on thick branches.

Specie	Type of vegetation	Altitude	Annual precipitation	Mean annual temperature
A. erubescens	Pine-Oak forest	2701 m a. s. l	772.5 mm	15–20°C
L. speciosa	Oak forest	2350 m a. s. l	1041 mm	16.4°C
L. caritensis	Subtropical moist forest	400 m a. s. l	1000-2000 mm	18–24°C
L. eltoroensis	Dwarf forest	700–1074 m a. s. l	5000 mm	18.5°C

TABLE 3. Demographic statistics of *E. crista-galli* during the period 2004–2005. The same letter indicates no significant difference (Tukey test).

	Growth rates			
	Number of pseudobulbs (psuedobulbs/individual/year)		Height of pseudobulbs (cm/individual/year)	
	SD	UR	SD	UR
Seedling (s)	0.222 ± 0.548a	0.000	0.368 ± 0.263a	0.200
Juvenile (j)	0.455 ± 0.522a	0.231 ± 0.439a	0.337 ± 0.109ab	0.592 ± 0.712a
Reproductive (r1)	1.417 ± 1.042b	0.375 ± 0.518a	0.185 ± 0.339b	0.163 ± 0.521ab
Reproductive2 (r2)	0.509 ± 1.948a	0.983 ± 1.105b	−0.087 ± 0.376c	0.223 ± 0.513b

304 died during July of 2004 to July of 2005; of those, 26% looked dried and 74% had disappeared. In UR, of the 549 individuals, 330 died during the same time; of those, 5% looked dried and 95% had disappeared. By stage, seedling and juvenile individuals had the highest mortality rates (TABLE 4), while reproductive stages showed the lowest mortality rates for both populations.

By calculating the transition matrixes (TABLE 4), λ values of 0.521 ± 0.134 for SD and 0.398 ± 0.268 for UR were obtained. In both cases the λ values were inferior to one, which indicates that the populations were decreasing. The stable stage structures (*w*) in both cases were dominated by reproductive individuals, which presented the highest reproductive values (*v*). The highest elasticity values were for the permanence of the reproductive$_2$ (TABLE 5), followed by the permanence of the reproductive$_1$ in the case of UR and by the transition of reproductive$_1$ to reproductive$_2$ in SD.

While comparing the elasticity indices of the different orchid species (FIGURE 1), we can see that in general stasis is the demographic process that most influences the destiny of the populations, and that fecundity has a relatively low influence on the behavior of λ. The highest value of elasticity for growth was obtained by *A. erubescens* (0.354), due principally to the incorporation of new individuals through vegetative propagation (0.162), which is contemplated as a type of clonal growth under the scheme of Silvertown et al. (1993).

The reproductive individuals are the ones which dominate the population behavior of epiphytes orchids, with the exception of *A. erubescens* for which it is the destiny of the non-reproductive individuals that has a greater influence over the destiny of the populations as a whole (FIGURE 2).

DISCUSSION

The epiphytic environment is characterized in general by low water and nutrient availability, which limits growth rates (Benzing 1990, Zotz 1998). However, Chase (1987) and Chase et al. (2005) commented that twig epiphytes present a higher growth rate which permits them to reach sexual maturity in less than a year, in spite of the greater fluctuations in water availability, a high luminosity, and lower availability of nutrient in the twig environment. When we compare the average growth rate of *E. crista-galli* individuals (0.68 ± 0.378 cm/year SD and 0.239 ± 0.527 cm/year UR) with that reported for *D. emarginata* (0.900 ± 1.63 cm/year), an epiphyte that reaches more than 40 cm of height at maturity (Zotz 1998), we found that it has higher growth rates than *E. crista-galli,* suggesting that twig epiphytes do not necessarily have higher growth rates than other epiphytes.

Ericina crista-galli reaches sexual maturity at

TABLE 4. Lefkovicht matrices of *E. crista-galli* in SD (a) and UR (b), during 2004–2005. Categories as in Table 1. n = number of individual per stage, w = stable stage structure, v = reproductive value, qx = death rate

a)	s	j	r_1	r_2	w	v
	0.000	0.000	0.004	0.062	0.092	0.204
	0.195	0.000	0.000	0.000	0.034	0.138
	0.171	0.120	0.053	0.040	0.107	0.318
	0.073	0.100	0.435	0.447	0.766	0.340
n =	41	50	246	226		
qx =	0.561	0.780	0.508	0.451		

b)	s	j	r_1	r_2	w	v
	0.000	0.000	0.040	0.008	0.056	0.168
	0.250	0.063	0.000	0.004	0.047	0.267
	0.000	0.250	0.200	0.196	0.476	0.234
	0.000	0.094	0.120	0.252	0.422	0.331
n =	4	32	25	531		
qx =	0.750	0.594	0.640	0.540		

TABLE 5. Elasticity matrix of *E. crista-galli* in SD (a) and UR (b), during 2004–2005, Categories as in Table 1.

a)	s	j	r_1	r_2	b)	s	j	r_1	r_2
	0.000	0.000	0.001	0.058		0.000	0.000	0.029	0.005
	0.015	0.000	0.000	0.000		0.035	0.007	0.000	0.004
	0.030	0.008	0.011	**0.058**		0.000	0.025	**0.205**	**0.178**
	0.014	0.007	**0.096**	**0.702**		0.000	0.013	0.174	**0.324**

the age of one year, while *D. emarginata* matures at six to ten years, *Encyclia tampensis* at 15 years or more, and *A. erubescens* after 12 years (Larson 1992, Zotz 1998, García 2003). This difference could be attributed to the minimum size required for the first reproduction to take place. In the case of *E. crista-galli,* individuals can reproduce at 0.4 cm of pseudobulb size, compared with the 3.5 cm of the pesudobulb size of *Lycaste aromatica,* 4 cm for the pseudobulbs of *A. erubescens* (García-Soriano 2003), the 4.5 cm for the pseudobulbs of *E. tampensis* (Hernández-Apolinar 1992), or 5 cm for *D. emarginata* (Zotz 1998). Rather than having higher growth rates, the precocity of *E. crista-galli* could be more linked to the minimum size necessary to reproduce. As mentioned by Benzing (1990), the reduction of organs and the fusion of functions (photosynthetic roots, foliar trichomes with absorption capacity) favor the optimization of resources by epiphytes and extremely so for twig epiphytes.

For orchids, recruitment of new individuals is infrequent (Larson 1992, Zotz 1998, Winkler & Hietz 2001, García-Soriano 2003) due mainly to the fact that the dust seeds lack endosperm and alone have insufficient reserves with which to support the developing embryo (Dressler 1990). To compensate this, they established a parasitic association with mycorrhizal fungi which provide nutrient to the embryo (Yoder et al. 2000, Batty et al. 2001, Otero et al. 2005). *Erycina crista-galli* is no exception, as the recruitment of new individuals was also found to be low in this study.

Generally, in every plant, and specifically in epiphytes, the youngest individuals have the highest mortality rates (Benzing 1981, Hernández-Apolinar 1992, Larson 1992, and Hietz 1997), as in our case. Low survival rates observed in the individuals of initial stages are a function of their susceptibility to hydric stress during the dry season (Benzing 1981, Hernández-Apolinar 1992, Larson 1992, Hietz 1997, Tremblay 1997, Zotz 1998, García-Soriano 2003, and Mondragón et al. 2004).

The mortality of juveniles of *E. crista-galli* (j = 78% SD and 59% UR) was higher than that reported for other species of epiphytic orchids. For example García-Soriano (2003) reported 45% survival in juvenile individuals of *A. erubescens,* while Zotz (1998) reported 50% survival of infantile individuals of *D. emarginata.* This highest mortality rate that we found in *E.*

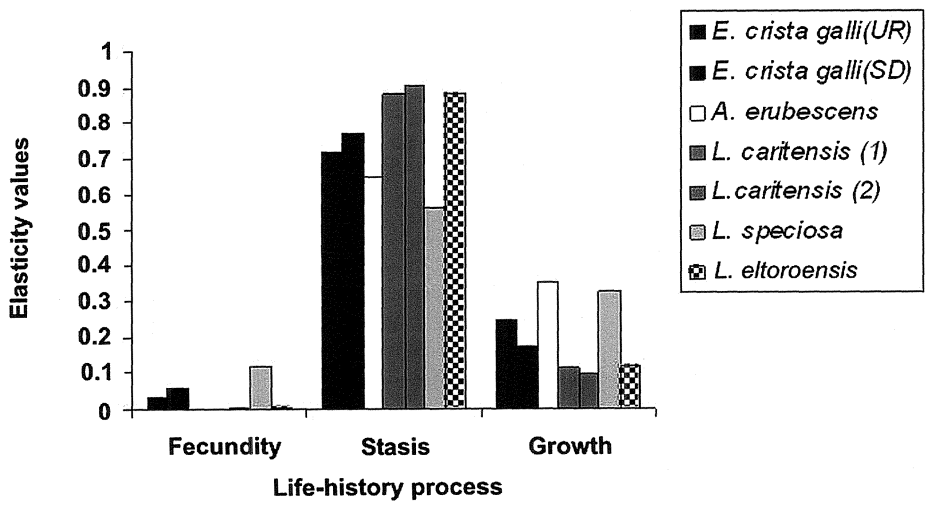

FIGURE 1. Added elasticity values by life-history process, for the orchid species evaluated.

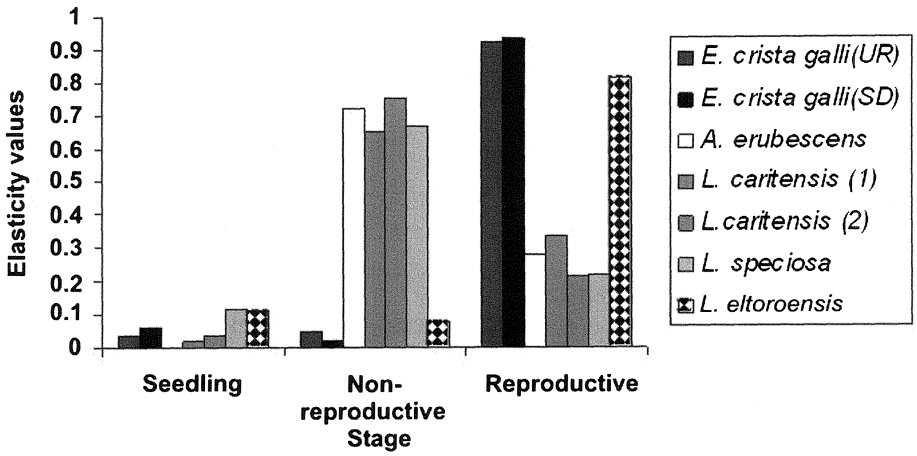

FIGURE 2. Added elasticity values by stage, for the orchid species evaluated.

crista galli could be caused by the high number of individuals that fell from the tree.

Due to the death of more than the half of the individuals sampled in SD (54%) as well as in UR (56%) in 2004, together with the low recruitment rates, the values of λ are inferior to one, suggesting that the populations are decreasing, contrary to that reported for populations of other epiphyte orchid species (*L. caritensis* λ = 0.995 and 0.999; *L. eltoroensis* λ = 0.998; *A. erubensis* λ = 1.024; and *L. speciosa* λ = 1.170), which are very close to the equilibrium, or increasing slightly as in the case of *L. speciosa* (Hernández-Apolinar 1992, Tremblay 1997, García-Soriano 2003, and Tremblay & Hutchings 2003).

It is important to consider that although we sampled individuals of *E. crista-galli* growing on coffee bushes, which is an imported species established in Mexico a little more than one century ago, this species also grows on other tree species (11 different species approximately, pers. obs.), either native or introduced species used as shade trees or as living fences to delimit plots of land. This has important implications for the permanence of these species in the region. First, the other trees can be considered as a "refuge" for *E. crista-galli* individuals, for they are less rigorously managed and have greater life expectancies (over 20 years) compared to the coffee bushes (the practice of the coffee culture requires the replacement of a coffee plant after five to eight years to maintain the production, depending upon the variety). And second, the seeds produced by the adult individuals of *E. crista-galli* that grow in those "refuge-trees" replenish populations living on the coffee bushes and may disperse to permit the colonization of other coffee plantations.

This necessity for repeated colonization by means of vagile seeds seems to be reflected by the elasticity values reported for fecundity in *E. crista-galli,* which are superior to most of those reported for other orchids whose substrates are more stable (Tremblay 2001, García-Soriano 2003, and Tremblay & Hutchings 2003), except to *L. speciosa* which presents the highest fecundity elasticity value (0.119). However, the permanence of trees is ephemeral if compared to the permanence of the soil (Bennet 1992). Therefore for epiphytes, repeated colonization of new branches and new hosts is essential to ensure the permanence of their populations (Benzing 1990, Zotz 1998), and for that reason the survival of reproductive individuals that ensure seed production is of vital importance (elasticity values), and even more so when recruitment is so infrequent.

It appears that there is no one demographical characteristic that distinguishes clearly between orchids that live attached to thin branches (twig epiphytes) and other epiphytic orchids. However, *E. crista-galli,* serving as a model of a twig epiphyte, reaches the age of sexual maturity at one year, while for other orchids it takes at least five years for the first sexual reproduction to take place. It is important to mention, however, that few studies have been carried out and our comparisons included very few species. Furthermore, the literature regarding demography of epiphytes using matrix models is particularly scarce, and it is well-known that the demographical behavior varies through time. Hence, studies ideally should be long-term and incorporate this variability (Moloney 1986, Mondragón et al. 2004). Unfortunately, it was not possible to continue our study, for the UR site was eliminated completely due to the floods in October 2005

caused by hurricane "Stan." At the same time the population in SD was reduced to 20 individuals, because the owner of the plantation decided to renew his coffee bushes and cut down old bushes, including 80% of those included in the census. Notwithstanding, this study permits us to catch a glimpse of the life-cycle and adaptation of twig epiphytes that live in highly unstable conditions at the extremes of epiphytism.

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